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THE EFFECT OF VARIOUS CARBON SOURCES
ON THE GROWTH OF SINGLE-CELLED CYANOPHYTA

I.A. Avilov, E.S. Sidorenkova

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16. Abstract In 19 strains of unicellular blue-green algae, belonging to genera <u>Synechococcus</u> , <u>Synechocystis</u> , <u>Aphanocapsa</u> and <u>Aphanothece</u> , the capacity of growth under mixotrophic conditions in mineral media with organic carbon sources (carbohydrates, polyols) was investigated. At moderate light intensity (1200 lx) and 0.5% of carbon source there was revealed: 1. Stimulation of growth; 2. Partial or complete inhibition of growth; 3. No influence of carbohydrate and polyols on the growth of some algae strains. Three physiological groups for the investigated strains have been outlined on the basis of data obtained. The possibility of using the differences revealed in classification of unicellular blue-green algae is discussed.			
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The Effect of Various Carbon Sources
On the Growth of Single-Celled Cyanophyta

I.A. Avilov, E.S. Sidorenkova

In spite of the fact that cyanophyta dwell in soil and ponds, sometimes rich with organic matter, ^{they} are encountered in exo- and endo-associations with plants and animals (mushrooms, filament algae, bryophyta, ferns, gymnospermae, angiospermae, protozoa) and, as do other phototropic organisms, can also maintain viability during prolonged periods of darkness, they have long been classified with essential-autotrophic microorganisms, which are incapable of assimilating organic carbon sources [Wildon D.C., Rees T., 1965; Holm-Hansen O., 1968]. The majority of the attempts to grow cyanophyta in heterotrophic conditions have concluded without success. However, even in 1917 Harder [Harder R., 1917] reported on the heterotrophic growth of Nostoc punctiforme, an endophytic organism separated from the roots of Hunnera sp. Subsequently, growth in darkness was detected near free-living structures of Nostoc muscorum [Allison F.E. e.a., 1937], on Tolypothrix tenuis [Kiyohara T. e.a., 1960], Chlorogloea fritschii [Fay P., 1965], Anabaenopsis circularis [Watanabe A., Yamamoto J., 1967]. In recent investigations by Khoja and Whitton [Khoja T.M., Whitton B.A., 1975], it was shown that many strains of filamentous cyanophyta are capable of heterotrophic growth in mediums with sucrose, fructose, glucose, and maltose.

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During a reaction in sucrose, all aspects investigated by the author fell into three types: those not reacting in its presence, and those growing photo-heterotrophically and chemo-heterotrophically. At the same time, it is notable that the strains, incapable of growth in darkness, did not possess a mucilaginous sheath, and those that grew in the darkness had mucilaginous sheaths or produced a thick mucilaginous environment. Currently, /98 more than 30 types of filamentous and more than 10 strains of single-celled cyanophyta have been observed which are capable of heterotrophic growth [Rippka R. e.a., 1979, Gusev M.V., Nikitina K.A., 1979]. In their papers, a series of investigators have also shown that carbohydrates can increase the growth of cyanophyta in light. At the same time, in certain investigations it has been reported that strains of the type Lyngbya lagerheimii, Anabaena variabilis, Agmenellum quadruplicatum and Aphanocapsa can grow in a medium with glucose and weak lighting, insufficient for the maintenance of photoautotrophic growth [Baalen C. e.a., 1971; Ohki K., Katon T., 1975]. Thus, in spite of the fact that cyanophyta are represented as types of organisms with comparatively close physiological characteristics, their separate representations can actually be distinguished by a series of physiological traits and, in part, by their relation to the carbon source or energy source. These distinctions can be of interest in the solution of the problem of the classification of cyanophyta, especially if the fact that the existing system of classification of these microorganisms is totally founded on their morphological characteristics is taken into account. Therefore, in the last ten years all the attention of investigators has been

directed even more toward the study of the physiological and biochemical variety of cyanophyta and the determination of the possibilities of using similar differences for improving the classification of their separate groups [Stanier R.Y. e.a., 1971; Stanier R.Y., 1975; Khoja T.M., Whitton B.A., 1975; Rippka R. E.a., 1979]. In the process of this work in separating and purifying cultures of cyanophyta, a series of bacteriologically pure strains of single-celled structures of the genera Synechocystis, Synechococcus, Aphanocapsa and Aphanothece were derived. In the current investigation this permits the recording of observations on the effect of various carbon sources on the growth of the strains studied and a determination of the prospects for the utilization of the pertinent characteristics for classification of single-celled cyanophyta.

Methodology. In a group of the investigated cultures, strains of the following types were isolated: Synechocystis minuscula No. 564, 578, 610, 611, 701, 713 -- Gromov strains, Synechocystis salina No. 553, 554, 567 -- Gromov strains, Synechocystis sp. No. 600, 555 -- Gromov strains, Synechococcus leopoliensis No. 257 -- Kratz a. Allen strains, No. 602 -- originator unknown, Synechococcus eximia No. 726 -- Gromov strain, Synechococcus schmidlea No. 670 -- Hindak strain 70/11, Synechococcus sp. No. 535 -- Gromov strain, Aphanocapsa sp. No. 751, 752 -- Gromov strain, Aphanothece bullosa No. 533 -- originator unknown (all strains from the collection of algae of the Peterhoff Biological Institute). Classification of the cultures are arranged according to morphological criteria [Efremova L.P., Avilov

I.A., 1978], proceeding on the principle formulated by Komarek [Komarek J., 1976] Axenic cultures of algae were incubated in test tubes (7 ml. medium) in a liquid mineral medium No. 6 [Gromov B.V., 1965]. In experiments on the effects of various organic carbon sources on the growth of the cultures, one of the following sugars (0.5%) were added to the mineral medium No. 6: glucose, galactase, fructose, maltose, sucrose, lactose, arabinose, rhamnose, or polyol (0.5%): mannitol, sorbitol, dulcitol. Concentrated solutions of these mixtures (10%) in distilled water were sterilized twice by a flowing steam (for 1 hour) and were added in the necessary quantity to the test tubes with medium No. 6. Having been seeded, they were prepared with 7-day cultures of the autotrophically bred algae. The quantity of seeded material did not exceed 90 mg/l of dry cell matter. Then, the test tubes were placed in a luminostat and at an exposure of 1200 lux were /99 bred over the course of 14 days at a temperature of 25° C. The accretion of the biomass of cells was determined turbidimetrically in a spectrophotometer SPH-2 at 560 nm. All of the experiments were executed in triplicate with four parallel samples in one experiment. The average arithmetical values of the twelve measurements are presented in the table. The error of the average value did not exceed 5-7%.

Results. For a preliminary characterization of the possible reaction of the algae on the carbohydrate in a medium on a sample of three strains (No. 600, 610, 670), which belong to different species, the character of the effect of different concentrations of organic substrata on the growth of cyanophyta in light was determined. From the data in Table 1 it is apparent that at a

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0.1% concentration of carbohydrates the growth of Synechocystis sp. No. 600 is not distinguished from the control (medium of), and in the presence of polyol it varies: in mannitol the growth is weaker, and in sorbitol and dulcitol it is significantly higher than the control, while with an increase of concentration to 0.5% the biomass accretion increases. With an increase of concentration of all mixtures to 1% the development of the culture either begins to slow, or is totally suppressed. Two other strains disclosed a similar reaction at higher carbohydrate concentrations (1%). On the strength of this case as a comparison of the strains of all collections in a medium, carbohydrates and alcohols were introduced in a 0.5% concentration. At such a quantity of organic substrata there is observed acceleration, deceleration or complete suppression of growth and also the absence of the effect of organic carbon sources on the growth of the algae (see Table 1).

Table 1.
The Influence of Various Carbon and Polyhydric Alcohol Concentrations on the Growth of Cyanophyta (at g/l) in Light (1200 lux)

a. Среда	Synechocystis sp. № 600				Synechocystis minuscula № 610				Synechococcus schmidtea № 670			
	0.1%	0.25%	0.5%	1%	0.1%	0.25%	0.5%	1%	0.1%	0.25%	0.5%	1%
Среда № 6 (K)	3,8	3,8	3,7	3,7	4,3	4,4	4,2	4,3	3,6	3,6	3,7	3,5
K + глюкоза	3,8	3,9	3,9	0,0	4,9	4,8	4,8	0,0	3,7	3,5	5,0	0,0
K + галактоза	3,7	3,5	3,4	0,0	4,5	4,4	4,5	0,0	4,0	3,9	4,0	0,0
K + фруктоза	3,6	2,6	0,0	0,0	1,7	0,0	0,0	0,0	4,0	3,9	4,1	0,0
K + мальтоза	4,0	2,8	0,0	0,0	4,5	4,6	5,0	0,0	3,7	3,9	3,9	0,0
K + сахароза	3,7	4,2	4,5	3,6	4,3	3,6	3,6	3,5	3,2	3,5	3,5	3,3
K + лактоза	3,9	3,6	3,6	0,0	4,0	3,8	3,5	0,0	3,1	3,0	2,6	0,0
K + арабиноза	3,6	3,6	3,8	0,0	4,6	4,5	4,4	0,0	3,6	3,6	3,7	0,0
K + рамноза	3,5	3,8	3,4	0,0	4,4	3,9	4,0	4,0	2,9	3,1	3,4	2,3
K + маннит	3,2	3,5	3,5	3,4	4,0	0,0	0,0	0,0	3,8	2,8	2,6	0,0
K + сорбит	4,4	4,7	5,0	3,5	4,3	3,9	4,0	4,0	3,4	3,3	5,1	4,3
K + дульцит	4,8	4,8	4,9	3,4	4,1	4,1	4,1	4,3	3,4	3,6	5,5	4,6

a. Medium b. Medium No. 6 (K) c. glucose d. galactose
e. fructose f. maltose g. sucrose h. lactose i. arabinose
j. pannose k. mannitol l. sorbitol m. dulcitol

The results of determining the character of the growth of the studied strains of single-celled cyanophyta in light in a mineral medium with the addition of 0.5% of one of the tested carbohydrates and polyol are presented in Table 2. As can be seen from the data in the table, the strains tested are distinguished by the accretion of the biomass in mineral medium No. 6. Included are those showing a slowly increasing biomass accretion (strains No. 533, 553, 554, 555), which for 14 days did not exceed 2 g/l, and the intensively growing (3.7-4.2 g/l). The remaining strains occupy intermediary places according to intensiveness of growth. The addition of various carbon sources affect in different ways the development of the tested cultures. Disaccharide maltose /100 produces the most stimulating effect on the growth of many strains (12 strains) from carbohydrates. In three cultures (No. 533, 564, 713) the accretion of cell mass was 80-125% more than in the control, for five strains (No. 611, 701, 535, 751, 752) -- 30-40%, for four others (No. 578, 610, 554, 555) -- 20-27% higher in comparison to the control, and finally, the growth of four strains (No. 600, 257, 567, 726) in the presence of this source suppressed it to a significant degree or totally. The growth of the remaining three strains (No. 553, 670, 602) did not change in the presence of maltose. Glucose, galactose, rhamnose, and arabinose also stimulated the accumulation of biomass on many tested strains (6-8 strains). Along with this, as in the case of the maltose, for certain cultures the existence of these carbohydrates results in partial or total suppression of growth. It should be noted that fructose produces an inhibiting effect on the development of the majority of tested strains (12). In only

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three strains (No. 535, 611, 533) there is observed a stimulation of growth in a medium with this carbohydrate.

Table 2.

The Influence of Various Carbon Sources (Carbohydrates, Alcohol) on the Phototrophic Growth (in g/l) of Single-Celled Cyanophyta

а. Среда	Pos. <i>Synechocystis</i>										Pos. <i>Synechococcus</i>					Aphanocapsa sp.		Aphanothera lalleia	
	<i>S. minuscula</i>					<i>S. subtilis</i>		<i>S. hantzschii</i>	<i>S. leopoldinae</i>	<i>S. rubra</i>	<i>S. mediterranea</i>	535	751	752	533				
	504	578	610	611	701	713	551									554	557		555
б. Среда № 6 (К)	2,8	2,6	4,2	3,2	3,7	3,2	2,0	2,0	3,4	2,0	3,7	2,6	2,9	2,8	3,7	2,8	3,6	3,2	1,6
в. К+глюкоза	3,6	2,8	4,8	4,3	2,8	5,0	2,0	3,8	2,7	3,9	3,9	1,6	2,1	3,0	5,0	4,7	2,8	4,9	1,9
г. К+галактоза	3,0	2,8	4,5	4,2	4,1	3,2	2,5	3,2	3,2	2,9	1,4	1,7	2,2	2,5	4,0	3,6	4,2	3,3	2,5
д. К+фруктоза	0,5	3,3	0,0	4,7	0,3	2,5	0,5	1,2	1,7	0,4	0,0	1,6	2,3	3,6	4,1	4,6	0,7	0,5	3,1
е. К+мальтоза	5,0	3,3	5,0	4,2	4,8	6,1	2,2	2,5	1,8	2,5	0,0	1,9	2,2	2,5	3,9	3,9	4,9	4,6	3,6
ж. К+сахароза	2,5	2,3	3,6	3,2	3,7	3,9	1,9	2,8	2,6	2,0	1,5	2,3	3,5	3,0	3,5	2,8	2,5	4,1	1,6
з. К+лактоза	2,9	2,6	3,5	4,0	3,3	3,0	1,7	2,6	2,3	2,1	3,6	1,8	1,8	2,5	2,6	3,8	4,4	3,3	1,9
и. К+арабиноза	3,0	1,1	4,4	4,0	4,2	2,0	2,6	3,2	3,1	3,1	3,8	1,8	2,0	2,5	3,7	3,9	4,0	3,8	2,0
й. К+рамноза	4,0	3,0	4,0	3,1	4,2	3,9	1,8	2,9	3,2	2,5	3,4	1,6	3,4	3,0	3,4	3,4	4,3	3,6	1,7
к. К+маннит	2,1	2,8	0,0	3,8	1,0	3,0	1,6	2,9	3,5	2,3	3,5	2,2	2,4	2,5	2,6	2,5	3,3	2,6	2,0
л. К+сорбит	2,5	3,3	4,0	4,1	2,7	3,0	1,5	1,7	2,8	2,5	5,0	1,9	0,8	0,9	5,1	2,2	4,2	3,1	2,0
м. К+дульцит	3,1	3,5	4,1	3,5	3,9	3,5	2,0	2,7	2,0	2,5	4,9	1,9	1,5	3,1	5,5	2,1	3,7	3,2	1,9

a. Medium No. 6 (K) b. Medium No. 6 (K) c. glucose d. galactose
e. fructose f. maltose g. sucrose h. lactose i. arabinose
j. ramnose k. mannitol l. sorbitol m. dulcitol

From the data of Table 2 it is apparent that with the breeding of cultures of cyanophyta in a mineral medium in light when an addition of any of the tested carbon sources is made the following can be expected: 1) an acceleration of growth, 2) a partial or total suppression of it, 3) the absence of an effect on the growth of the culture. In Table 3 the results of the investigation according to the highly enumerated quantitative differences in the character of the action of the carbohydrates on the growth of the algae. In the following table conventional notation has been adopted: +++ -- accretion in the medium with carbohydrates higher then in the control by 50-100%; ++ -- exceeding the control by 30-49%; + -- exceeding by 20-29%; K - a

value close to the control; P -- partial or complete suppression of growth. In Table 3 the strains are grouped not in relation to their systematic classification, but in relation to the similarity of the revealed physiological characteristics. Presented at the beginning of the table are groups of strains (No. 554, 611, 535, 555, 713, 752, 564, 533) characterized by their capacities for more intensive growth in the mediums with glucose and maltose than in medium no. 6. The majority of the representatives of this group grow more intensively in medium No. 6 with galactose (4 strains), ramnose (5 strains) and arabinose (4 strains), and such substrata as sucrose, lactose, mannitol, sorbitol and dulcitol, promote accelerated growth of single strains. The case of /101 partial or complete suppression of growth with the tested substrata (excluding fructose) are rare here. It is possible to relate the representatives of this group to glycophylic structures. In a systematic relationship this group is represented by five strains of the genus Synechocystis (No. 554, 611, 555, 713, 564), by one strain of genus Aphanocapsa (No. 752) and by one strain of genus Synechococcus (No. 535). Out of the five strains of Synechocystis, three are related to the type S. minuscula (No. 564, 611, 713), one to the type S. salina (No. 554), and one to an undetermined classification. Most likely, it is possible to relate the glycophylic structures and Aphanothece bullosa (No. 533), however, the growth of this strain does not quicken with glucose.

At the end of the table is arranged a group of strains which are characterized in practice by the fact that their growth

Table 3.
The Distribution of Strains of Single-Celled Cyanophyta by Physiological
Groups Depending on Their Relationship to Organic Carbon Sources

a. Углеродная группа	I					II					III				
	54	61	535	555	713	732	741	531	679	578	642	690	551	731	730
О. Льюкоза	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++
Д. Галактоза	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++
Е. Фруктоза	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++
И. Рамноза	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++
К. Арабиноза	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++
Л. Мальтоза	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++
Г. Сахароза	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++
Ж. Лактоза	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++
З. Маннит	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++
И. Сорбит	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++
К. Дульцин	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++

a. Carbons b. Alcohols c. glucose d. galactose e. fructose
f. ramnose g. arabinose h. maltose i. sucrose j. lactose
k. mannitol l. sorbitol m. dulcitol

begins to slow or ceases completely in the presence of all tested carbon sources. Two strains enter into this group of the type Synechococcus (No. 257, 726) and one strain of Synechocystis (No. 567). It is possible to add two strains of Synechocystis minuscula (No. 751). The remaining cultures constitute a group of structures, which in the majority of cases, do not react to carbohydrates in a medium, although here there are noted solitary instances of suppression or stimulation of growth in light. By species and genus the composition of this group is also mixed. Strains of genus Synechocystis (No. 553, 600, 578) predominate, but there are also strains of the genus Synechococcus (No. 602), Aphanocapsa (No. 751) and Aphanothece (No. 533).

The results of our investigation show that mixotrophic growth of tested single-celled structures at moderate lighting provide glucose, galactose, ramnose, arabinose, lactose, sucrose, /102 and in particular maltose. In our former works [Avilov I.A., Sidorenkova E.S., 1977] it was shown that the enumerated carbohydrates stimulate growth of filamentous cyanophyta. At the same time, it was noted that the character of the action of the carbohydrates and polyhydric alcohol on the growth of filamentous structures depends on the concentration of the substrata. As can be seen from the data of the present investigation, the action of the carbohydrates on the growth of single-celled structures also depends on the concentration of the substrata. This circumstance forces one to refer with definite precaution to the literature on trophism of this and other structures of cyanophyta, since various investigations have used different concentrations of carbohydrates in their works: 1% glucose [Kenyon e.a., 1971]; 0.5%

glucose [Pelroy e.a., 1973]; 0.25% glucose [Stanier R.Y. e.a., 1971].

Speaking of prospective uses of the characterizations of nourishment of single-celled cyanophyta for their classification, it is necessary to note that according to the complex of studied criteria, it is observed that there are differences not only between strains of different types of genera and types, but between strains of the same type. So, among 6 strains of the type Synechocystis minuscula are those whose growth is stimulated in light by many carbohydrates and alcohols (No. 611, 713), and strains whose growth is blocked by separate substrata partially and totally (No. 701). From the three strains of Synechocystis salina, one (No. 554) clearly appears as a distinct glycopylic structure, the growth of another (No. 567) is suppressed by almost all carbohydrates and alcohols, and a third strain (No. 553) occupies an intermediate position. From the five strains of the type Synechococcus, it is difficult to find two between them that react similarly on a carbohydrate in the medium. Even two morphologically similar strains S. leopoliensis (No. 257, 602) are significantly distinctive in the reaction on carbohydrates and alcohol. There is a sufficiently great difference between two strains of the type Aphanocapsa (No. 751, 752).

Thus, according to the results of our investigation, it is possible only to discuss the existence of definite physiological groups of single-celled cyanophyta, represented by strains of various classified positions. One group -- the glycopylic strain (No. 554, 611, 535, 555, 713, 752, 564, 533; see Table 3)

-- is characterized by the fact that the growth of all of its representatives is significantly accelerated by glucose and maltose, and the remaining carbohydrates stimulate growth of separate structures. Another group --the glycophobic strain (No. 257, 567, 726 and possibly, 610, 701, 751) -- are characterized by the fact that the growth of these algae is suppressed partially or totally by glucose, fructose, maltose, lactose, sorbitol, and dulcitol. It is possible to relate the remaining five strains to the mesophyllis structure (group II, Table 3), which is observed in separate instances, either stimulating or depressing growth.

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